

# Ant–plant–homopteran mutualism: how the third partner affects the interaction between a plant-specialist ant and its myrmecophyte host

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By estimating relative costs and benefits, we explored the role of the homopteran partner in the protection mutualism between the myrmecophyte *Leonardoxa africana* T3, the ant *Aphomomyrmex afer*, and sap-sucking homopterans tended by ants in the tree's swollen hollow twigs. The ants obtain nest sites and food from their host-plant (food is obtained either directly by extrafloral nectar or indirectly via homopterans). *Aphomomyrmex* workers patrol the young leaves of *L. africana* T3 and protect them against phytophagous insects. Because ants tended, either solely or primarily, coccids in some trees and pseudococcids in others, we were able to study whether the nature of the interaction was dependent on the identity of the third partner. First, the type of homopteran affects the benefits to the tree of maintaining a large ant colony. Larger colony size (relative to tree size) confers greater protection against herbivory; this relationship is more pronounced for trees whose ants tend pseudococcids than for those in which ants tend coccids. Second, for trees (and associated ant colonies) of comparable size, homopteran biomass was much larger in trees harbouring coccids than in trees with pseudococcids. Thus, the cost to the tree of maintaining ants may be greater when ants are associated with coccids. The net benefits to the plant of maintaining ants appear to be much greater with pseudococcids as the third partner. To explore how the type of homopteran affects functioning of the system, we attempted to determine which of the resources (nest sites, extrafloral nectar, and homopterans) is likely to limit ant colony size. In trees where ants tended coccids, ant-colony biomass was strongly dependent on the number of extrafloral nectaries. In contrast, in trees whose ants tended only pseudococcids, colony biomass was not related to the number of nectaries and was most strongly determined by the volume of available nest sites. We present hypotheses to explain how the type of homopteran affects functioning of this symbiosis, and discuss the implications of our study for the evolutionary ecology of ant–plant–homopteran relationships.

**Keywords:** mutualism; ant–plant interactions; ant–homopteran interactions; conditional interactions; tropical forest

## 1. INTRODUCTION

Most symbioses between ants and myrmecophytes involve a third partner: sap-sucking homopterans tended by ants (Davidson & McKey 1993). Ants eat homopterans and/or their honeydew (Way 1963; Carroll & Janzen 1973; Buckley 1987). Such tripartite relationships are mutualisms if the net benefits are reciprocal, i.e. if, for each partner, the benefits of the interaction are greater than the costs. Benefits for ants are quite evident: the plant provides nest sites and food resources, either directly through extrafloral nectar or production of specialized food bodies, or indirectly via the homopterans. Homopterans benefit by having exclusive access to the host's sap in sheltered sites protected from predation, and are sometimes completely dependent on ants (Gullan & Kosztarab 1997). In most cases, the main advantage for the plant is protection against herbivores or against competing plants (Janzen

1972; Stout 1979; Fiala *et al.* 1989; Longino 1991; Fonseca 1993; Maschwitz & Fiala 1995).

Cushman & Beattie (1991) and Bronstein (1994) have emphasized the importance in studies of mutualism of measuring costs and benefits. However, with some notable exceptions (e.g. Pellmyr 1989; Herre & West 1997), few studies have done this. Most studies of tripartite ant–plant–homopteran symbioses, for example, have been concerned with demonstrating that ants and their associates benefit the plant. Attempts to estimate the costs imposed on the plant by ant-tended homopterans are mostly lacking. This is surprising, because dependence on homopterans imposes costs that are not incurred by myrmecophytes that feed their ants directly. First, homopterans are sometimes plant disease vectors (Chung Kim & McPherson 1993). Second, the presence of homopterans inserts an additional trophic level, increasing the energy cost of ant maintenance. Third, colonization of myrmecophytes by founding queens is a risky affair (McKey 1988), and may be even riskier when ants depend on homopterans. When successful

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initiation of the symbiosis requires the encounter and establishment of three partners, rather than two, the problems are multiplied.

There has also been little attempt in studies of tripartite symbioses to examine variation that may affect costs and benefits to the plant. This lack is also surprising. In loose, facultative associations between ants, plants and homopterans, the effect on the plant is often highly variable, the outcome ranging from strong mutualism to parasitism, depending, among other factors, on the type of homopteran involved (Cushman 1991; Cushman & Addicott 1991). Is the same true for homopteran-mediated symbiotic interactions? The present study deals with an ant-plant-homopteran symbiosis in which we tried to take into account these two neglected aspects of tripartite symbioses: the costs of homopterans to the plant, and the effect of variation in homopteran association on the outcome of ant-plant interactions.

We studied the myrmecophyte *Leonardoxa africana* T3 (Chenuil & McKey 1996), associated with the ant *Aphomomyrmex afer*. In contrast to the strictly bipartite interaction between *L. africana* sensu stricto and *Petalomyrmex* (McKey 1984; Gaume *et al.* 1997), *Aphomomyrmex* in *L. africana* T3 is associated with homopterans, and it is the role of the latter that is the focus of this study. Two species of homopterans, a coccid and a pseudococcid, are tended by *Aphomomyrmex* in domatia of the host, but each tree and ant colony is associated, solely or predominantly, with one or the other species. Throughout this paper, we will refer to *L. africana* T3 simply as *Leonardoxa*.

To investigate the functioning of these tripartite symbioses, we adopted the following approach.

1. To examine the importance of homopteran trophobionts in maintaining the tree's ant colony, we compared the number of foliar nectaries in this plant and *L. africana* sensu stricto, in which homopterans are absent and all ant food resources are produced directly by the plant.
2. We determined whether maintaining a larger ant colony relative to tree size benefits the plant.
3. We examined whether benefits and costs to the plant of maintaining ants are different depending on the type of homopteran tended by ants.
4. We explored which of the three resources provided to ants by the plant, either directly (nest sites, extrafloral nectar) or indirectly (homopterans), best determines ant-colony biomass and is thus most likely to limit colony growth.
5. We asked whether, in these homopteran-mediated interactions, the plant can control its investment in maintenance of the ant colony. To do this, we attempted to identify the factor limiting the biomass of homopterans supported by the plant.

In each of these aspects, we compared interactions mediated by the two types of homopterans.

## 2. MATERIAL AND METHODS

*Leonardoxa africana* T3 (Leguminosae: Caesalpinioideae) is an understory tree of rainforest in the Southwest Province of Cameroon. Like the closely related species *Leonardoxa africana* sensu stricto (McKey 1984), the tree possesses swollen, hollow

internodes inhabited by ants, and provides extrafloral nectar which they consume (McKey 1991). Only mature leaves produce nectar. Saplings are occupied by diverse species of ants, but adults are exclusively inhabited by *Aphomomyrmex afer*. This ant tends homopterans inside the domatia, the coccid *Houardia abdita* and/or the pseudococcid *Paraputo anomala*. Neither *H. abdita* nor *P. anomala* is host-specific (see, respectively, Hodgson 1990; Entwistle 1972). *Aphomomyrmex* workers actively patrol young leaves of the host, and experiments show that they attack and kill phytophagous insects placed on young leaves (Gaume & McKey 1998). Like the symbiosis between *L. africana* and *Petalomyrmex* (Gaume *et al.* 1997), the interaction between *L. africana* T3 and *Aphomomyrmex* is a protective mutualism.

The studied trees come from a population of *Leonardoxa* in Korup National Park (Southwest Province of Cameroon; latitude 5°0' N, longitude 8°50' E). A total of 21 trees and their insect colonies were collected, 10 in January 1996 and 11 in November 1996. Each tree was cut, then sectioned domatia by domatia, and the sections were put in 95% ethanol. For each tree, we counted the numbers of leaves and leaflets (leaves are pinnately compound, with usually 3–4 pairs of leaflets) and the number of foliar nectaries, and scored the amount of herbivory (*H*, percentage of foliar surface removed by chewing insects) to each leaflet on the following scale: 0, leaflet completely intact; 1, 0 < *H* ≤ 25% eaten; 2, 25 < *H* ≤ 50%; 3, 50 < *H* ≤ 100; 4, leaflet missing. For each tree we calculated a mean percentage of herbivory to leaflets, using for each leaflet the median percentage value of its herbivory class. As a conservative measure, we excluded missing leaflets from this estimate, because they may have fallen for reasons other than herbivory. Our measure of herbivory is thus likely to be an underestimate. As each domatia was dissected, we measured its internal diameter, *a*, and its length, *b*, estimating its volume as that of a cylinder:  $(a/2)^2 b$ . We summed the volumes of all domatia to estimate the total volume available in the tree. We removed, counted, and sorted all ants and homopterans, dried them in an oven at 40 °C for 8 h, then weighed them to determine total biomass of ants and of homopterans for each tree.

Using ANOVA, we found that there was no effect of month of collection on any of the parameters measured. There was also no effect of month on the proportion of colony biomass accounted for by alates and alate brood. We therefore lumped January and November samples in all further analyses.

All 21 trees contained homopterans in association with *Aphomomyrmex*. In ten trees, ants tended only the pseudococcid, and in four others, only the coccid. In seven trees, *Aphomomyrmex* tended both homopterans, but in all cases coccids were strongly predominant. Pseudococcids accounted on average for only 15.1% of homopteran biomass in these mixed associations. We first applied general linear models to our complete data. The independent variables were quantitative variables and the factor was type of homopteran, which we first divided into three categorical variables (coccids, pseudococcids and mixed). These analyses revealed two points. First, in each case, 'coccid' and 'mixed' colonies behaved similarly and significantly differently from colonies tending only pseudococcids. We thus lumped 'coccid' and 'mixed' colonies in all further analyses and compared these (henceforth designated as colonies tending coccids) with colonies tending only pseudococcids. Second, the interactions between this factor and the quantitative variables were almost always significant. Thus, in all further analyses we treated separately those trees in which ant colonies tended only or predominantly coccids and those in

which ants tended only pseudococcids. The analyses were done using SAS v. 6.12 (SAS Institute 1996), taking into account tests of type III.

Ant-colony biomass may be a good estimator of colony fitness, because it reflects both the quantity of alates produced (reproduction) and the quantity of workers (growth). In order to know which of the three types of resources we measured (volume of nest sites, foliar nectar and homopterans) most limited colony biomass, we performed for each of the two groups multiple regressions aimed at explaining the dependent variable 'colony biomass' as a function of the three quantitative variables. Selection by descending sequences revealed the variable that best explained 'colony biomass' and was thus most likely to be the limiting factor. Stepwise regressions gave the same results as backward regressions, showing that the selected models were robust.

We then conducted similar analyses, separately for the two groups, to determine the factor limiting each type of homopteran. Two kinds of factors are likely to limit homopteran biomass: (i) size of the ant colony, because ants are often suspected to regulate populations of associated homopterans (Buckley 1987); and (ii) resources (nest-site and food availability). For this model the dependent variable was biomass of homopterans and explanatory variables were number of workers, domatia volume and number of leaflets (which reflects photosynthetic surface and hence supply of sap).

Simple regressions were also performed for each of the two groups. To examine whether identity of the homopteran influenced the relationships, we compared regression slopes for both groups using *t*-tests (corrected for unequal variances (Sokal & Rohlf 1981, p. 411)), the results of which are presented mostly in the figure legends. Analogous *t*-tests comparing the intercepts revealed that they were never significantly different between groups for any of the regressions performed.

### 3. RESULTS

In contrast to the interaction between *L. africana* sensu stricto and *Petalomyrmex* (McKey 1984), nectar is a relatively unreliable resource for *Aphomomyrmex* in *L. africana* T3. Indeed, the mean number of nectaries per leaflet varied from 0.02 to 0.69 among the trees studied. The mean of tree means was 0.28 (s.d.=0.19, *n*=21 trees, nectaries counted on 8897 leaflets). This value is much lower than in *L. africana* sensu stricto (Ebodie population studied by Gaume *et al.* (1997): mean of tree means=2.65, s.d.=0.41, *n*=17 trees, 1347 leaflets counted). Number of nectaries per leaflet is not only significantly lower in *L. africana* T3 (Mann-Whitney  $U_{\min}=0$ ,  $p<0.0001$ ), but also much more variable among trees (coefficient of variation=67.3%, compared with 15.6% for *L. africana*). Some trees have almost no nectaries. In addition, compared with *L. africana* sensu stricto, fewer nectaries are active, and rates of nectar production by active nectaries are lower for this plant (L. Gaume, unpublished data). In contrast to nectaries, homopterans were present and abundant in each of the studied trees and appear to be necessary partners of the ants in this plant. They can be of two kinds, either a coccid (*Houardia abdita*) or a pseudococcid (*Paraputo anomala*).

Ants benefit the plant by patrolling and protecting young leaves against phytophagous insects (Gaume & McKey 1998). In both groups, herbivory decreased with

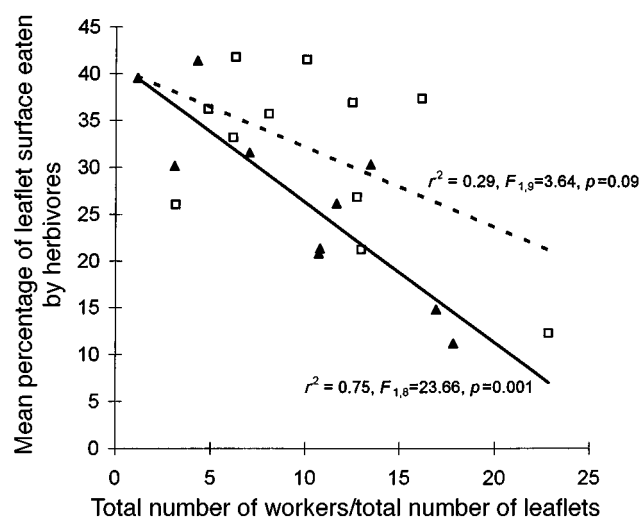


Figure 1. Regressions of herbivory as a function of the patrolling potential of workers for coccid- and pseudococcid-tending colonies. Open squares, coccids; filled triangles, pseudococcids; broken line, linear regression for coccids; bold line, linear regression for pseudococcids.

increasing density of ant occupation (number of workers relative to leaflet number), indicating that denser colonies conferred greater protection. However, this relationship was much stronger for colonies tending pseudococcids than for colonies tending coccids (figure 1). For the latter, the regression between herbivory and number of workers per leaflet was only marginally significant ( $r^2=0.29$ ,  $F_{1,9}=3.64$ ,  $p=0.09$ ). For colonies tending pseudococcids, in contrast, the regression was highly significant ( $r^2=0.75$ ,  $F_{1,8}=23.66$ ,  $p=0.0012$ ). Arcsin (square root) transformation of the variable herbivory (a proportion), carried out to normalize the data, did not change the results ( $r^2=0.32$ ,  $F_{1,9}=4.17$ ,  $p=0.07$  for coccid-tending colonies;  $r^2=0.75$ ,  $F_{1,8}=24.08$ ,  $p=0.0012$  for pseudococcid-tending colonies). Colonies tending pseudococcids protected their host trees against herbivores more effectively than did colonies tending coccids.

Not only were benefits to the plant greater when ants tended pseudococcids, but also the cost of maintaining ants appeared to be lower. Ant-colony biomass increases linearly with total domatia volume of the tree and the slope of the regression is virtually the same for both groups (figure 2a). However, ant biomass, which increases with homopteran biomass, increases more rapidly with colonies tending pseudococcids than with colonies tending coccids (figure 2b). If homopteran biomass reflects the amount of sap removed, then for plants and ant colonies of comparable size, the cost of maintaining ants may be greater for plants with coccids. The identity of the homopteran trophobiont thus appears likely to influence both costs and benefits to the plant of maintaining protective ants.

We then attempted to identify mechanisms that could explain how the identity of the third partner affects costs and benefits. For each of the two groups (ants and trees with coccids, ants and trees with pseudococcids), we first determined whether each resource variable was correlated with ant-colony biomass. For colonies tending coccids, simple regressions showed that colony biomass was positively correlated with volume ( $r^2=0.51$ ,  $F_{1,9}=9.55$ ,

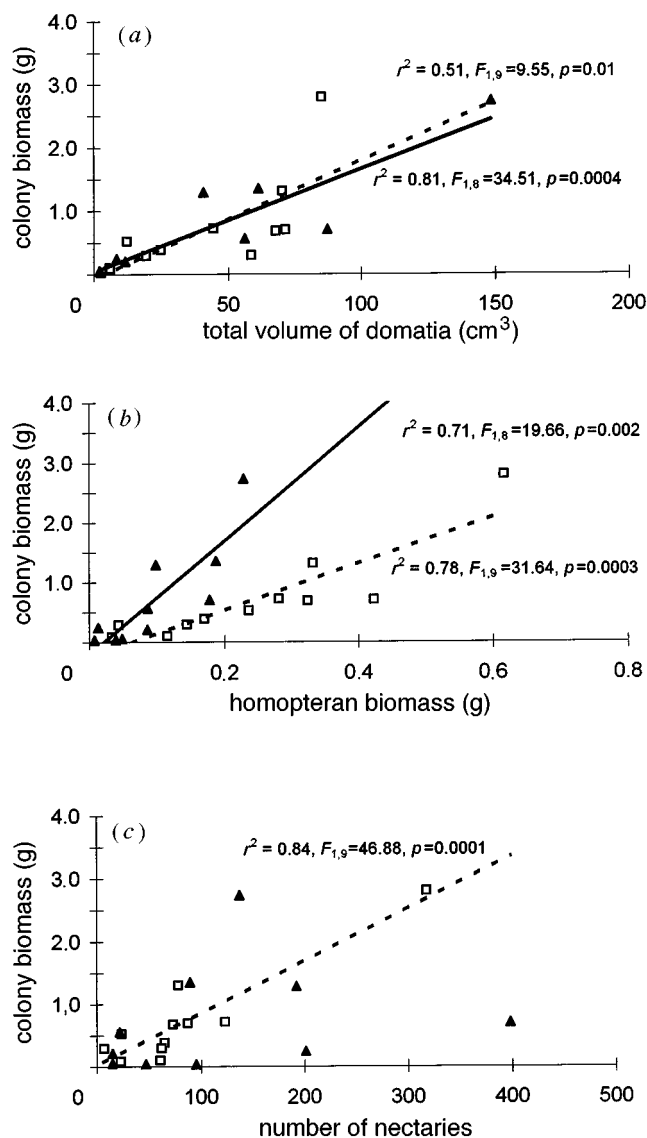


Figure 2. (a) Regressions between colony biomass as a function of total volume of domatia for coccid- and pseudococcid-tending colonies. Slopes of regressions for the two groups are not significantly different ( $t$ -test,  $t = 0.38$ , d.f. = 19,  $p = 0.71$ ). (b) Regressions between colony biomass as a function of homopteran biomass for coccid- and pseudococcid-tending colonies. Slopes of regressions for the two groups are significantly different ( $t$ -test,  $t = 2.47$ , d.f. = 19,  $p = 0.02$ ). (c) Relation between colony biomass and number of nectaries for coccid and pseudococcid-tending colonies. Open squares, coccids; filled triangles, pseudococcids; broken line, linear regression for coccids; bold line, linear regression for pseudococcids.

$p = 0.013$ , figure 2a), homopteran biomass ( $r^2 = 0.78$ ,  $F_{1,9} = 31.64$ ,  $p = 0.0003$ , figure 2b), and number of nectaries ( $r^2 = 0.84$ ,  $F_{1,9} = 46.88$ ,  $p = 0.0001$ , figure 2c). Each of the resources offered by the tree to the ants may contribute to colony growth. However, these variables are all inter-correlated. According to backward selection applied to the full model, ant-colony biomass was best explained by the number of nectaries. Thus, when ants tended coccids, colony biomass appeared to be limited by the number of nectaries. As with coccids, when ants tended pseudococcids colony biomass was positively correlated with volume ( $r^2 = 0.81$ ,  $F_{1,8} = 34.51$ ,  $p = 0.0004$ , figure 2a) and

with pseudococcid biomass ( $r^2 = 0.71$ ,  $F_{1,8} = 19.66$ ,  $p = 0.0022$ , figure 2b). In contrast, there was no correlation between colony biomass and the number of nectaries ( $r^2 = 0.06$ ,  $F_{1,8} = 0.47$ ,  $p = 0.51$ , figure 2c). Nectar thus appeared to be a relatively unimportant resource for colonies tending pseudococcids. Backward selection on the full model revealed that for pseudococcid-tending colonies, the factor that appeared to limit colony growth was volume.

We performed similar regression analyses to determine the factor limiting homopteran biomass. For both types of homopteran, each of the studied variables (number of workers, total volume of domatia and total leaflets) is positively correlated with homopteran biomass (figure 3a–c). The factor that best explained homopteran biomass was the number of workers in the ant colony, for both coccids (figure 3a,  $r^2 = 0.90$ ,  $F_{1,9} = 77.35$ ,  $p = 0.0001$ ) and pseudococcids (figure 3a,  $r^2 = 0.86$ ,  $F_{1,8} = 50.93$ ,  $p = 0.0001$ ). Analyses thus indicate that the plant has only indirect control of homopteran biomass. Either nectaries ('coccid' colonies) or domatia volume ('pseudococcid' colonies) limits the size of the ant colony, whose workers in turn limit homopteran biomass.

#### 4. DISCUSSION

Our results show that the identity of the homopteran trophobiont strongly affects the relationship between the ant colony and its host-plant. Costs and benefits to the plant of ant association, as well as the factors limiting ant-colony biomass, all appeared to depend on the type of homopteran.

First, herbivory is reduced with increasing number of workers relative to photosynthetic surface, suggesting that increased 'patrolling potential' brings increased benefit. Workers patrol young leaves day and night, driving away or killing most of the phytophagous insects they encounter (Gaume & McKey 1998). But this protection is far less efficient when ants tend coccids (figure 1).

Second, our data indicate that cost of maintaining ants may be greater when ants tend coccids rather than pseudococcids. Plants harbouring coccids support about three times as much homopteran biomass for the same domatia volume (figure 3b), and about 2.5 times as much homopteran biomass for the same ant biomass (figure 2b), as do plants harbouring pseudococcids. This estimate of relative cost must, however, be viewed with caution. Although homopteran biomass may be correlated with the amount of resources taken from the plant within a single homopteran species, the relationship between homopteran biomass and cost to the plant may not be the same for different homopteran species. Differences in feeding location within the plant may lead to differences in the nature and the amount of plant tissues ingested and/or assimilated. Differences in life history (e.g. lifespan and metabolic rates) of the two sap-sucking insects may imply that an equivalent biomass of the two species represents different costs in terms of the resources taken from the plant.

In the presence of coccids, benefits to the plant of maintaining ants are lower than in the presence of pseudococcids, whereas costs may be greater. The relationship is thus closer to a parasitism when the ants tend coccids than when they tend pseudococcids. Symbiotic

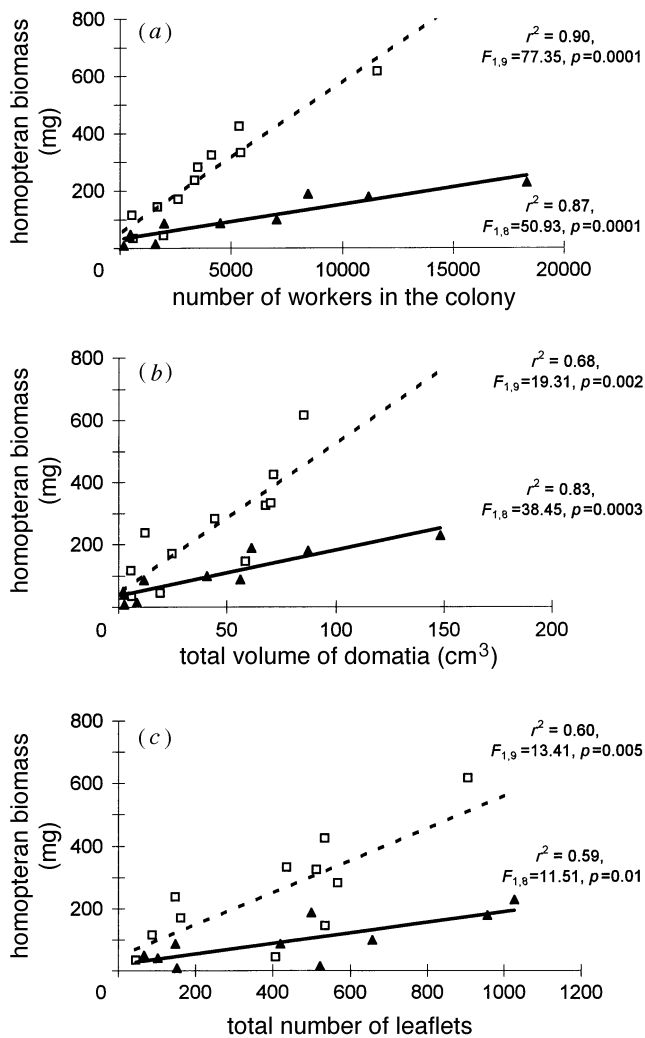


Figure 3. (a) Regressions between homopteran biomass as a function of number of workers for coccid- and pseudococcid-tending colonies. The slopes of regressions for the two groups are significantly different ( $t$ -test,  $t = 6.56$ , d.f. = 19,  $p = 0.000\ 001$ ). (b) Regression between homopteran biomass as a function of total volume of domatia for coccid- and pseudococcid-tending colonies. The slopes of regressions for the two groups are significantly different ( $t$ -test,  $t = 3.01$ , d.f. = 19,  $p = 0.007$ ). (c) Regressions between homopteran biomass as a function of number of leaflets for coccid- and pseudococcid-tending colonies. The slopes of regressions for the two groups are significantly different ( $t$ -test,  $t = 2.32$ , d.f. = 19,  $p = 0.03$ ). Open squares, coccids; filled triangles, pseudococcids; broken line, linear regression for coccids; bold line, linear regression for pseudococcids.

ant-plant relationships mediated by homopterans may thus have variable outcomes, as is the case for facultative homopteran-mediated associations (Cushman 1991). It is important to emphasize, however, that the tree's protective ants require homopterans, and that having ants with coccids is better for the tree than not having ants at all. The ant-plant-coccid relationship is still a mutualism, but with smaller net benefit to the plant.

Thirdly, identity of the third partner also changes the nature of factors limiting ant colony size. When ants tended coccids inside the domatia, the number of extrafloral nectaries was most limiting. By contrast, when ants tended pseudococcids, the factor that best explained

colony biomass was the total volume available inside the domatia, whereas there was no correlation with the number of nectaries.

For ants that construct their own nests, colony size is often limited by the quantity of trophic resources available in their foraging area. When ants nest in myrmecophytes, food resources are usually predictably present on the host plant, and colony size may be limited either by food or by space (volume available in the tree's domatia). When all food is provided directly by the plant—which also directly controls nest-site volume—food and space may be co-limiting. But when part of the ants' food is obtained from another source, e.g. homopterans tended by ants, space limitation may be more frequent than food limitation, for two reasons. First, the plant cannot directly control the quantity of sap removed by homopterans; ants and homopterans are likely to take more resources than if the plant directly controlled its investment. Second, homopterans also occupy space inside the domatia, increasing the likelihood of space limitation for ants.

Working with *Tachigali* occupied by *Pseudomyrmex* tending homopterans inside the tree's domatia, Fonseca (1993) showed that the volume available, rather than food resources (only homopterans in this case), was the factor most limiting colony growth. In *Leonardoxa* trees in which *Aphomomyrmex* tended pseudococcids, we also found that volume, rather than food resources, was the limiting factor. However, *Aphomomyrmex* colonies tending coccids were limited by nectar. This effect of type of homopteran on functioning of the system raises two immediate questions.

First, why are pseudococcid-tending colonies more limited by volume than are coccid-tending colonies? Among the possible explanations, the two most obvious ones can be excluded. Individual pseudococcids are smaller (adult length 3.5 mm) than coccids (4.5 mm), and for trees of comparable total domatia volume, the number (L. Gaume, unpublished data) and total biomass of pseudococcids is much lower than in trees with coccids (figure 3b). Pseudococcids thus occupy a lower, not greater, proportion of the volume available in their host trees than do coccids. Neither are pseudococcid-tending ant colonies larger relative to available volume than are coccid-tending colonies. The slope of the regression between ant-colony biomass and domatia volume is virtually the same for the two types of associations (figure 2a). Our data favour a third type of explanation: other factors (biomass of homopterans or number of nectaries) are less limiting when ants tend pseudococcids, and understanding the differential response to volume hinges on understanding differential responses to other resources. Differential response to homopteran biomass does not appear to be the key, because the coefficient of determination between this factor and ant-colony biomass is similar for the two types of associations (figure 2b). Furthermore, homopteran biomass is much lower relative to ant biomass for pseudococcid-tending colonies, suggesting that homopteran biomass should, if anything, be more limiting, not less, in this type of association. The most marked difference between the two types of associations is seen in their response to foliar nectaries (figure 2c). For coccid-tending colonies, the coefficient of determination between number of nectaries and ant-colony biomass was the highest observed for any resource for either of the two types of

associations. In strong contrast, there was no significant correlation between the number of nectaries and ant-colony biomass in trees where ants tended pseudococcids, the only such case of independence observed for either type of association for the three resources measured.

This leads to the second question: why is biomass of pseudococcid-tending colonies virtually independent of number of nectaries, whereas that of coccid-tending colonies depends strongly on this resource? Analyses of extrafloral nectar have generally shown it to be chemically similar to honeydew, with comparable quantities and types of sugars and amino acids (Way 1963; Auclair 1963; Bentley 1977; Becerra & Venable 1989). If this is true for extrafloral nectar of *Leonardoxa* and honeydew secreted by homopterans feeding on its sap, our results suggest that pseudococcids may produce larger quantities of honeydew, or honeydew of higher quality as food for ants, than do coccids. Supplied with ample or high-quality honeydew, pseudococcid-tending colonies would be independent of nectar.

Finally, our results show that the plant's control of how much it invests in these tripartite systems is indirect. Within each type of association, it appears that the ant colony is limited by a resource provided directly by the plant, either volume (colonies tending pseudococcids) or nectar (colonies tending coccids), and that ants in turn (rather than plant resources) regulate homopteran biomass (figure 3a). However, the most striking indication of the plant's limited control of its investment arises from comparison of the two associations: plants harbouring coccids support more homopteran biomass than do plants of comparable size with pseudococcids. Ants (and homopterans) have an interest in the survival and growth of the host-tree, so that selection would favour avoiding severe over-exploitation of the tree. However, the limits are probably set higher, especially in the case of ants tending coccids, than if the plant could set the limits itself. In view of these results, we present hypotheses aimed at explaining why costs and benefits for the plant to maintain its colony of ants differ according to the identity of the tended homopteran.

How can the difference in plant protection be explained? We suggest that patrolling activity is lower in coccid-tending colonies, and propose two hypotheses, which are not mutually exclusive, to account for this.

1. Coccids require more care from workers than do pseudococcids. For ant colonies and trees of similar size, the number and biomass of coccids are greater than that of pseudococcids, and a larger number of workers may be required for their care (figure 3a).
2. Ants obtain more protein from coccids than from pseudococcids, and thus less actively patrol young leaves in search of insect prey. There are two alternative ways in which ants might obtain more protein or amino acids from coccids. First, their honeydew may contain more of these nitrogenous substances. Second, ants may harvest more coccids directly. Few data are available comparing chemical composition of honeydew of different homopterans. Those that exist (Davidson & Patrell-Kim 1996) suggest that pseudococcid honeydew may be richer in amino acids than that of coccids. We thus find no support for the first alternative. On the

other hand, ants may prey on some species of homopterans and tend others (Buckley 1987). Predation upon trophobionts is likely to be lower for those which, like the pseudococcid *Paraputo anomala*, are covered with wax (Way 1963). Moreover, ants may be more likely to act as predators upon homopterans that produce lower amounts or lower quality of honeydew (Edinger 1985). If the coccid *Houardia* produces less or lower-quality honeydew than *Paraputo*, *Aphomomyrmex* may tend *Houardia* essentially for the protein in their bodies. Ants tending coccids would obtain more protein from their homopteran associates and would thus have less incentive to patrol young leaves in search of insect prey. This may explain why anti-herbivore protection is reduced in the presence of coccids. In contrast to some other mutualistic plant-ants (see Janzen 1967; Fiala *et al.* 1989; Fonseca 1993; Maschwitz & Fiala 1995), *Aphomomyrmex* workers attempt to capture and consume insects encountered on young leaves, rather than discarding them from the plant (Gaume & McKey 1998).

If the two homopteran associates of *Aphomomyrmex* in *Leonardoxa* do differ in honeydew production, the selective value of foliar nectaries would depend on the identity of the third partner. This could explain the great inter-individual variation in the number of nectaries we found in this taxon. When ants tend coccids, trees with numerous nectaries should be favoured, because their resident colonies, strongly dependent on this resource, have more workers per unit leaf area than trees with fewer nectaries, and the trees are thus better protected. These trees would be at a disadvantage when the resident colonies tend pseudococcids, because they would incur the costs of constructing nectaries and producing nectar without accruing any benefit. Varying direction of selection on nectary number would maintain polymorphism of this character in the population. As in other balanced polymorphisms, this outcome entails a certain degree of maladaptation, because there is no indication that the number of nectaries can directly influence the identity of the third partner, nor that the plant can respond to the type of homopteran by producing the appropriate number of nectaries. 'Mismatched' associations occur.

The hypotheses we propose to explain why plants incur greater costs and receive lower benefits when their ants tend coccids must be tested by further study in the field. Whatever the explanation for the patterns we observed, our results clearly show that the effect on the plant in this system depends on the identity of the homopteran partner, moving closer towards parasitism when ants tend coccids rather than pseudococcids. Selective interests of the plant and of its ant colony are not entirely congruent. Effect of identity of the homopteran partner on costs and benefits for ants may thus be different from those on the plant, and need to be explored. This is, to our knowledge, the first study that focuses on how the identity of a homopteran partner influences symbiotic interactions between ants and plants. Because most ant-plant symbioses involve homopterans (Davidson & McKey 1993), more work should be done to explore the role of homopterans in these systems.

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